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Vocal Diversity and Taxonomy of *Nomascus* in Cambodia

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It is usually thought that Nomascus gabriellae *is the only* Nomascus *sp. in Cambodia. We studied vocal diversity among different wild populations of* Nomascus *in Cambodia to assess their taxonomic relationships and to examine whether their vocal patterns correspond to forms previously described for* Nomascus leucogenys siki *and* Nomascus gabriellae. *We tape-recorded crested gibbon songs in southern Mondulkiri Province, in central Rattanakiri Province, and in 2 different districts of the Virachey National Park in northern Rattanakiri. We also tape-recorded typical songs of* Nomascus leucogenys siki *near the type locality of the taxon in the Bach Ma National Park in central Vietnam. We analyzed 40 song bouts from different gibbon groups, including 151 phrases of 33 females and 235 phrases of 39 males. Discriminant analyses revealed marked separation of the most southern songs (Mondulkiri) from those of all other localities. Vocal differences among the 3 gibbon populations in northeast Cambodia (Rattanakiri) are less pronounced; they do not differ more among each other than each of them differs from the northernmost sample from Bach Ma (Vietnam). Vocal characteristics of the study populations revealed no cline, and populations do not differ significantly in vocal variability. We conclude that Cambodian crested gibbons represent 2 distinct taxa: Those from southern Mondulkiri are* Nomascus gabriellae, *those from northeast Cambodia (Rattanakiri) closely correspond to the sample from Bach Ma (Vietnam) and, together with the latter, represent a different taxon. We provisionally assign them to* Nomascus leucogenys siki *because of the close geographic distance*

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between Bach Ma and the type locality of the taxon. We postulate that a taxonal boundary exists between southern Mondulkiri and central Rattanakiri and discuss the possible factors that may have acted as distribution barriers.

KEY WORDS: crested gibbons; diversity; hylobatidae; songs; *Nomascus*; systematics.

INTRODUCTION

All gibbon species produce elaborate, loud, long, and stereotyped patterns of vocalization often referred to as songs (Geissmann, 1993, 1995, 2002a, 2003; Haimoff, 1984a; Marshall and Marshall, 1976). Preferentially, gibbons utter song bouts in the early morning that last for *ca.* 10–30 min. In most gibbon species, mated individuals combine their respective songs into well-coordinated duets. Species-specific song characteristics in gibbons are largely genetically determined (Brockelman and Schilling, 1984; Geissmann, 1984, 1993; Marshall and Sugardjito, 1986; Mather, 1992; Tenaza, 1985). Researchers have previously demonstrated that song characteristics are useful to assess systematic relationships on the generic and the specific level and to reconstruct gibbon phylogeny (Creel and Preuschoft, 1984; Geissmann, 1993, 2002a, 2002b; Haimoff, 1983; Haimoff *et al.*, 1982, 1984; Marshall *et al.*, 1984).

Crested gibbons (*Nomascus*) are 1 of 4 main taxonomic groups within the Hylobatidae and are characterized by various morphologic, anatomic, karyologic, and vocal features (Geissmann, 1993, 1994, 1995; Geissmann *et al.*, 2000; Groves, 1972, 2001; Schilling, 1984a). Crested gibbons exhibit several unique characteristics in singing behavior that set them apart from other gibbons (Geissmann *et al.*, 2000 p. 43f). Song bouts of mated pairs of *Nomascus* are highly stereotyped, male-dominated duet song bouts, whereas only nonmated individuals appear to produce solo songs. Crested gibbons also exhibit the highest degree of sexual specificity in their songs because there is typically no overlap between the sexes in either note or phrase repertoire (Geissmann, 2002a).

Crested gibbons occur in tropical evergreen and less seasonal parts of semi-evergreen rain forests of Indochina (southern China, Vietnam, Laos, and Cambodia). Southern white-cheeked crested gibbons (*Nomascus leucogenys siki*) and yellow-cheeked crested gibbons (*N. gabriellae*), are restricted to the southern parts of the distribution range (Fig. 1) (Geissmann *et al.*, 2000).

Delacour (1951) and Groves (1972, 2001) regarded museum skins from Saravane and Savannaket (southern Laos) as intergrades between *Nomascus gabriellae* and *Nomascus leucogenys siki*, suggesting the occurrence of

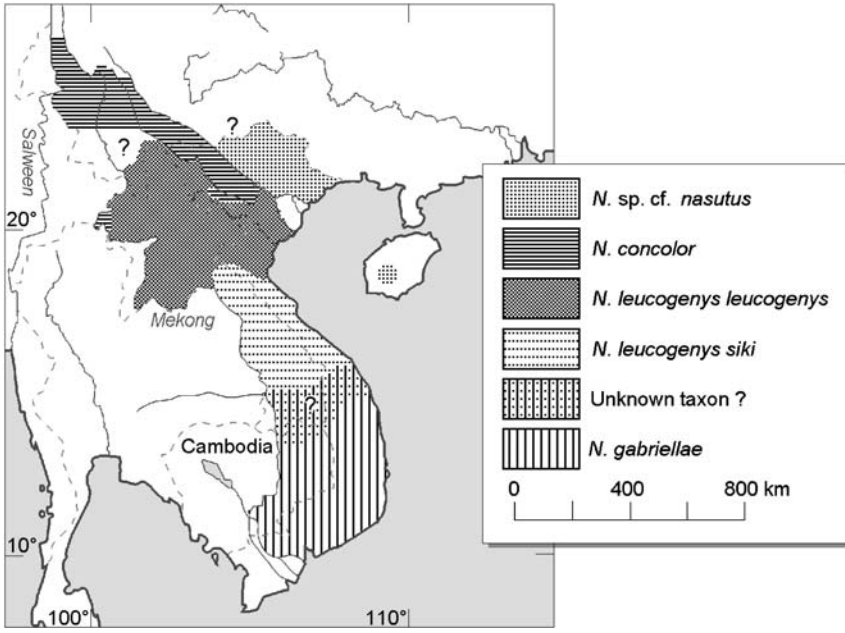

Fig. 1. Distribution of *Nomascus* spp. (modified from Geissmann *et al.*, 2000). Question marks refer to, from north to south, 1) the unknown survival (and identity) of Chinese gibbons east of the red river in Yunnan province, 2) a large apparent gap in the distribution area of gibbons in Yunnan province, and 3) the unknown identity of gibbons in a large area between the distribution areas of *Nomascus leucogenys* and *N. gabriellae*, respectively. Dashed lines indicate political boundaries.

a hybrid zone between them. Geissmann *et al.* (2000, p. 49) reexamined the museum specimens from Savannaket and found no conclusive evidence for intergradation, but only diagnostic characteristics of *Nomascus leucogenys siki*. However, gibbon songs from a large area extending from southernmost Laos and the Laotian Bolovens Plateau to southern central Vietnam including Bach Ma National Park clearly differed from *Nomascus gabriellae*, but also to a lesser extent from songs of zoo individuals of *N. leucogenys siki* (Geissmann, 1995; Geissmann *et al.*, 2000; Tallents *et al.*, 2001). Two gibbon song fragments tape-recorded in Virachey National Park in northeastern Cambodia suggest that a similar intermediate song type occurs there (Geissmann, unpublished data).

Geissmann (1995) and Geissmann *et al.* (2000) proposed that the large area (Fig. 1) either represents a broad intergrade zone in which the more southern taxon (*Nomascus gabriellae*) gradually replaces the more

northern one (*N. leucogenys siki*), or that a previously unrecognized taxon may occur therein. As Geissmann *et al.* (2000) noted, it is possible to test the 2 hypotheses: If a broad intergrade zone is the correct explanation, one would expect that gibbon songs exhibit a change in cline from the typical *Nomascus gabriellae* to the typical pattern of *N. leucogenys siki* as one moves from the area of *N. gabriellae* in the south to the area of *N. leucogenys siki* in the north. The absence of such a cline or a cline that is interrupted by larger areas in which song patterns remain stable may imply that previously unrecognized taxa occur in the large area.

We tested the 2 hypotheses for the Cambodian section of the crested gibbon distribution area. In Cambodia, crested gibbon distribution is restricted to the part of the country east of the Mekong River. The only taxon of crested gibbons in Cambodia is currently assumed to be the yellow-cheeked crested gibbon, *Nomascus gabriellae* (Baker *et al.*, 2002; Smith, 2001), though no museum specimen from the area exists and researchers have conducted no study on the morphological, genetic, or vocal characteristics of Cambodian crested gibbons.

We studied the vocal diversity of various local populations of crested gibbons in Cambodia. If all crested gibbon populations in Cambodia belong to *Nomascus gabriellae*, they should all exhibit the species-specific song characteristics typical of *N. gabriellae* and be a vocally homogeneous group, comparable to other gibbon populations of 1 taxon (Dallmann and Geissmann, 2001, 2006). We therefore first examined whether all study populations exhibited the same song pattern and the degree to which such a song pattern corresponded to, or deviated from, the patterns of *Nomascus gabriellae* and *N. leucogenys siki* that Geissmann *et al.* (2000) previously described.

Second, we tested whether the local populations differ in their intrapopulation song variability, because elevated phenotypic variability could indicate a hybridization zone.

Finally, we examined whether local call types—if they existed—follow a recognizable geographic pattern. A gradual change from a more *gabriellae*-like song pattern in the south to a more *siki*-like song pattern in the north would denote a large hybridization belt. Conversely, if song characteristics were stable over large areas and changed abruptly from 1 local population to another, a genetic boundary between 2 gibbon taxa likely exists. Evidence for genetic isolation between any 2 of our sample sites could help to locate a possible subspecific or specific boundary, which could be relevant for population management and conservation strategies in Cambodia.

Table I. Field sites, with coordinates, tape-recording dates, and identity of recordists

Locality	Province, region	Pooled samples	Coordinates	Survey and recording date	Conductor of survey and/or recordist[a]
Bach Ma NP	Thua Thien Hue, C Vietnam	Bach Ma	107°51′E, 16°13′N	April 2001	T. G.
Taveng District, Virachey NP	Rattanakiri, NE Cambodia	Taveng	107°18′E, 14°11′N	March 2003	R. K.
Veunsai District, Virachey NP	Rattanakiri, NE Cambodia	Veunsai	107°00′E, 14°12′N	March 2003	R. K.
Mas Village	Rattanakiri, NE Cambodia	Poey	107°08′E, 13°57′N	April 2003	R. K.
Khamaeng Village	Rattanakiri, NE Cambodia	Poey	107°00′E, 13°57′N	April 2003	R. K.
Lomphat District	Mondulkiri, CE Cambodia	Lomphat	106°41′E, 13°10′N	May 2003	R. K.
Samling LC Coupe 2A	Mondulkiri, SE Cambodia	Samling	Unknown	April 2000 and March 2002	F. G. and P. D.
Samling LC Coupe 3	Mondulkiri, SE Cambodia	Samling	106°56′E, 12°09′N	April 2002	T. G.
Samling LC Coupe 5	Mondulkiri, SE Cambodia	Samling	106°55′E, 12°15′N	Jan. 2003	R. K.

C = central; E = east; LC = logging concession; NE = northeast; NP = national park; SE = southeast.
[a]P. D. = Pete Davidson; F. G. = Frédéric Goes; T. G. = Thomas Geissmann; R. K. = Roger Konrad.

METHODS

We followed the gibbon taxonomy of Geissmann (2002b) and Roos and Geissmann (2001), according to whom the 4 main divisions of Hylobatidae are genera. *Nomascus* comprises 4 species (*N. concolor, N.* sp. cf. *nasutus, N. gabriellae,* and *N. leucogenys*). *Nomascus leucogenys* includes the subspecies *N. l. siki*.

Field Methods

Our tape-recordings of gibbon songs originated from 4 different areas in Cambodia (by R. Konrad in 2003 and T. Geissmann in 2002) and from 1 area in Vietnam (by T. Geissmann in 2001) (Table I and Fig. 2). We also surveyed a further area in Cambodia (Lomphat Wildlife Sanctuary), but obtained no gibbon recording there. Because most recording sites were separated from each other by large geographic distances or geographic barriers, such as large rivers or extended areas of habitat not suitable for gibbons,

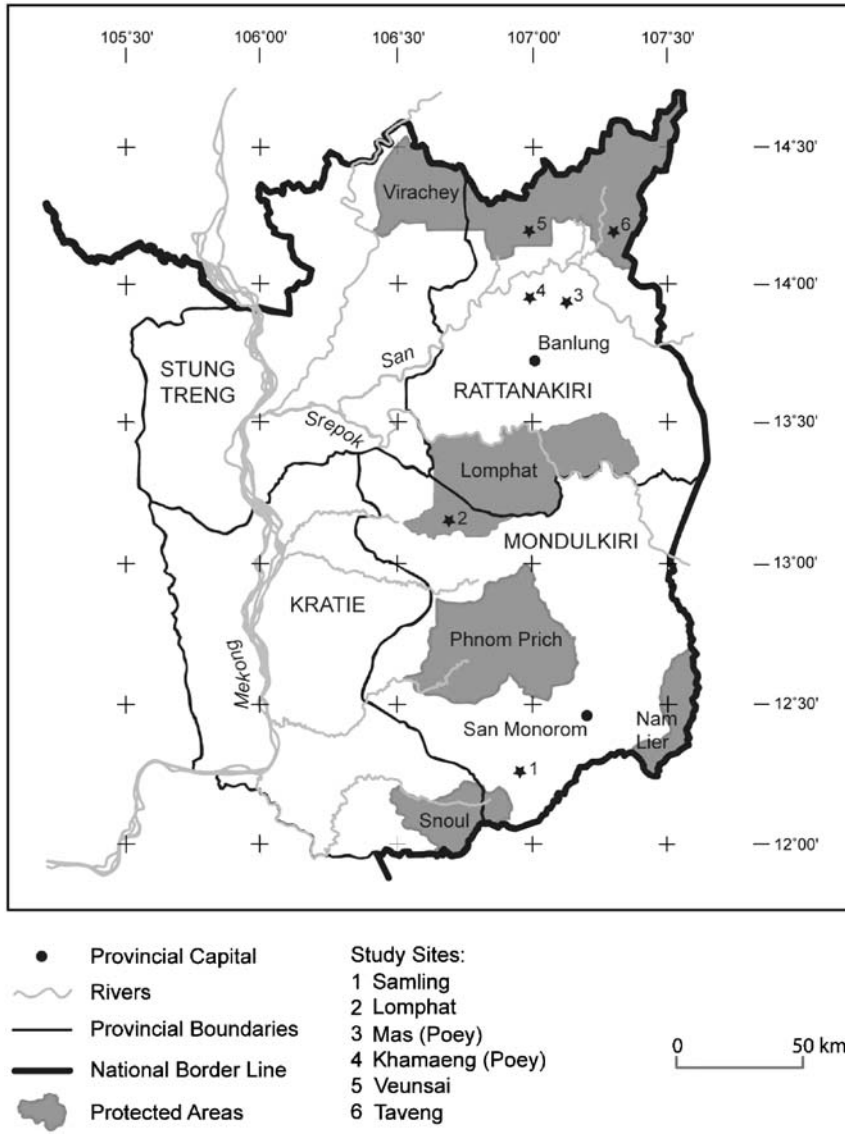

Fig. 2. Map showing the study sites in east Cambodia. (Adapted from Land cover representation, WWF-Cambodia, based on 1997 Landsat-TM images).

we regarded each of them as harboring a distinct gibbon population. We expected that analyzing the samples from Poey Commune, Veunsai District, and Taveng District separately (though they were situated within a

relatively short distance) would enable us to determine to what extent the presence/absence of the San River affects gibbon song structure.

Data Collection

Konrad made sound recordings with a SONY TCD-D8 DAT recorder and a SONY Electret Condenser Microphone ECM-MS957 (1-point stereo, unidirectional). Geissmann used a SONY WM-D6C cassette recorder with a JVC MZ-707 directional microphone and, alternatively, a SONY TC-D5M cassette recorder with a Sennheiser ME80 (+ K3U) directional microphone. We digitized the tape-recordings with a sampling rate of 22 kHz and a sample size of 16 bit. We generated sonograms (time *vs* frequency displays) of the sound material via the Canary version 1.2.4 software (Cornell Laboratory of Ornithology) on a Power Macintosh G4. We computed the sonograms by fast Fourier transformation (FFT). The FFT size of the sonograms was 2048 points with a time resolution of 256 points, overlap of 75%, frequency resolution of 10.77 Hz, and frame length of 1024 points (Charif *et al.*, 1995).

Nomascus Song Structure

Our acoustic terminology largely follows that proposed by Haimoff (1984a). The most relevant definitions for our study are in Table II.

The song structure of *Nomascus* spp. differs in several respects from that of other gibbons (Deputte, 1982; Geissmann *et al.*, 2000; Goustard, 1976; Haimoff, 1984b).

Female Song Contributions

Adult female *Nomascus* produce only great call phrases or fragments of great call phrases. Complete great call phrases consist of 3 phases: *oo* phase, bark phase (accelerando-part), and twitter phase (Fig. 3). The *oo* phase comprises long notes of slowly increasing frequency (*oo* notes, also termed fa notes in Schilling, 1984b). We arbitrarily defined *oo* notes by a frequency increase of ≤ 1 kHz/s. Subsequent notes are short, with a steep frequency increase of >1 kHz/s, and are termed bark notes (or fb notes), making up the bark phase of the great call. After the climax of the acceleration, bark notes tail off into the twitter phase (or fc notes). We did not take measurements for the twitter phase (last part of the great call), because twitter notes do not carry very far and the sonogram line is hardly visible for these notes.

Table II. Acoustic terms and definitions for gibbon song vocalizations

Term	Definition
Note	A single continuous sound of distinct frequency or frequency modulation that may be produced during either inhalation or exhalation
Element	A basic recognizable vocal unit of a single subject and composed of a single note or a short series of notes
Phrase	A single vocal activity consisting of a larger or looser collection of notes or elements or both; may be produced together or separately
Coda	A phrase produced by the male as a response to, and at or near the end of, the female's great call
Great call	The most stereotyped and most easily identifiable phrase of the gibbon song and produced by the adult females of all gibbon species
Great call sequence	Combination of the female great call and the corresponding successive coda of the male
Song	After Thorpe (1961, p. 15): A series of notes, generally of >1 type, uttered in succession and so related as to form a recognizable sequence or pattern in time
Song bout	All song notes of a gibbon group with periods of silence of <10 min
Solo song bout	Song bout produced by 1 individual (male or female) alone
Duet song bout	Song bout in which both sexes produce their loud sounds in an interactive manner (i.e., performing a mutually coordinated display)

Male Song Contributions

Fully developed song phrases of adult male *Nomascus* typically consist of 3 different note types (Fig. 3): 1) The boom notes (alternatively termed ma notes) are very deep notes of constant frequency and are produced during inflation of the throat sac. Crested gibbon males usually produce boom notes as single notes instead of short series or phrases typical of other male notes. 2) The *aa* notes (mb notes) are short, relatively monotonally repeated sounds, also referred to as staccato notes. 3) The most conspicuous part of the male song is the multimodulated phrase (mc notes), consisting of several notes that exhibit rapid and steep frequency modulations. Adult males typically utter a multimodulated phrase (coda) at or shortly after the climax of the female great call phrase.

In a fully developed duet song bout, the male singer continuously cycles through the 3 types of phrases (boom, staccato, and multimodulated—usually in this order). When the female starts a great call phrase, the male interrupts his song and, at the end of the great call, answers the great call with a coda. After that, he resumes cycling through the 3 phrases.

In the sonogram, note 1 of the male's multimodulated phrase exhibits a horizontal part followed by a trough part (Fig. 4). In the horizontal part the frequency remains at a relatively constant level. The trough part is characterized by a marked frequency decrease to the note frequency

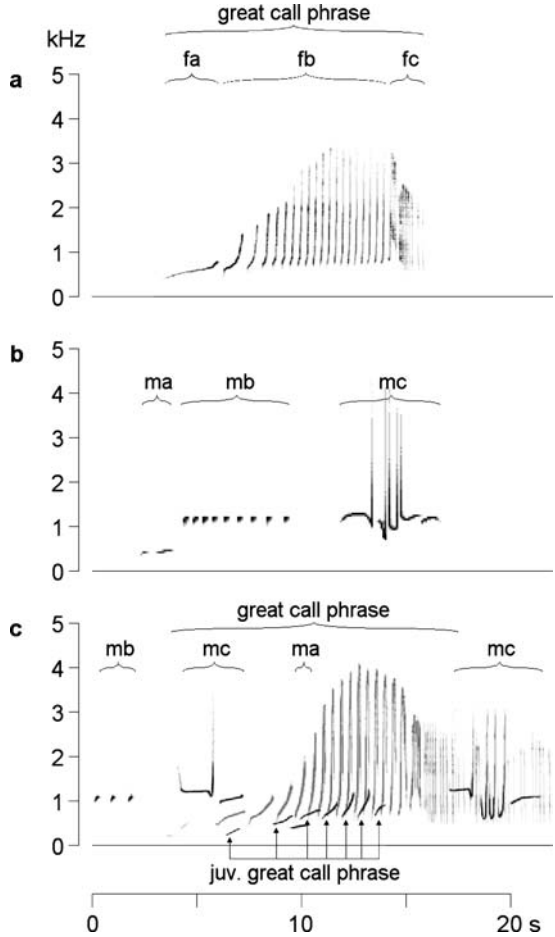

Fig. 3. Sonograms (fundamental frequencies only) showing sexual dimorphism in typical song phrases of the northern white-cheeked crested gibbon (*Nomascus leucogenys leucogenys*). **(a)** Great call phrase of an adult female. The great call begins with *oo* notes (fa), followed by barks (fb), and ends with twitter notes (fc).) **(b)** Phrases of an adult male. The sequence begins with booms (ma), followed by staccato notes (mb), and ends with a multimodulated phrase (mc). **(c)** Trio song of an adult pair and their juvenile son. The female sings a great call into the phrases of her mate, which pauses his song after a boom note (ma), and resumes singing by adding a multimodulated phrase (mc) to the end of the female's great call. During the great call, the female is accompanied with a short, great call-like phrase by her juvenile son. To facilitate reading of this sonogram, female contributions are artificially lightened and the juvenile phrase is darkened (from Geissmann *et al.*, 2000).

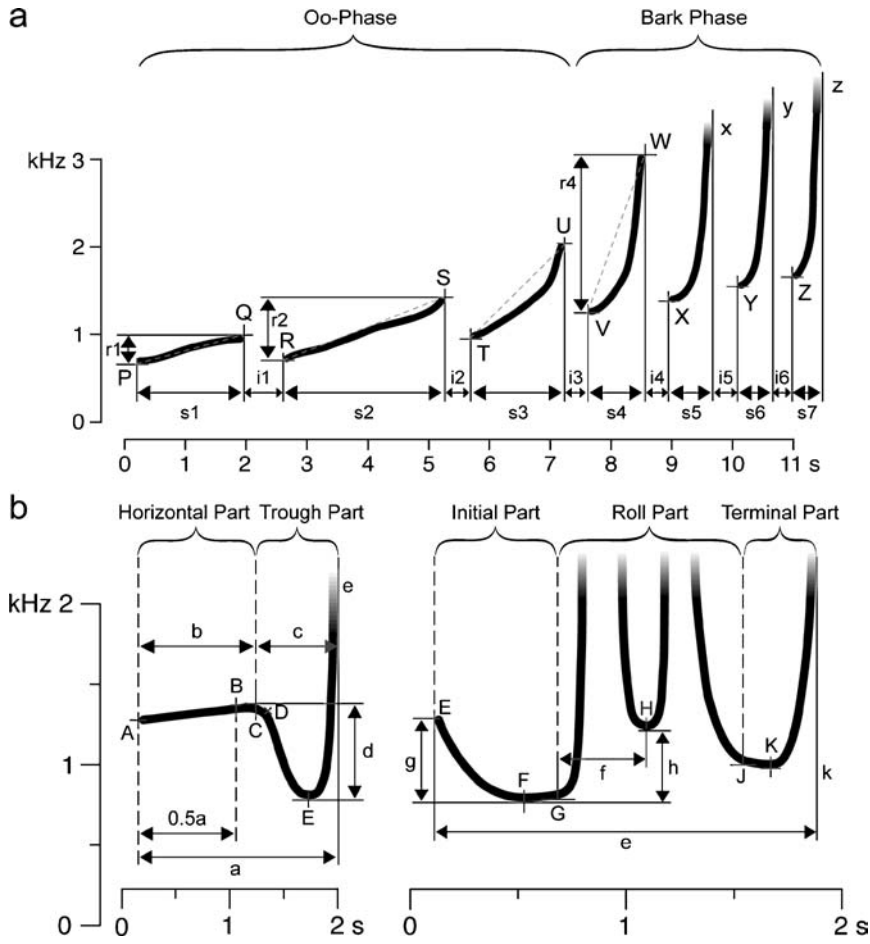

Fig. 4. Stylized sonogram (only fundamental frequencies shown) of **(a)** the female's great call and **(b)** the first and the second note of the male's multimodulated phrase, showing the split into different parts, all measurement points and tangents, durations, and ranges measured on these notes.

minimum and a subsequent rapid and steep increase (here termed terminal up-sweep).

Note 2 of the multimodulated phrase consists of 3 parts: initial part, roll, and terminal (Fig. 4). In the initial part the frequency decreases considerably and the sonogram line reaches a local frequency minimum. The roll part includes at least 1 rapid frequency modulation consisting of a steep up-and-down sweep (here termed roll). In the case of multiple rolls a short

trough occurs between 2 successive rolls. Most of the terminal part is characterized by a relatively constant frequency but exhibits a more or less pronounced frequency increase at the end of the note.

Note 3 may include 1 or several rolls as well, but generally, later notes of the multimodulated phase are simpler in structure, with no separate parts.

Sample Size of Tape-Recorded Gibbon Songs

We analyzed 40 song bouts (36 duet and 6 male solo songs) from wild, nonhabituated gibbons. The song bouts comprised 151 female phrases (great calls) from 33 different female gibbons (average: 4.6 phrases/individual) and 235 male phrases (92 of them codas) from 39 different male gibbons (average: 6 phrases/individual).

As the actual distribution of the group territories is unknown and the gibbon groups or individuals were generally out of sight during our tape-recording, we deduced the identity of the tape-recorded individuals from indicators such as position of the singer, simultaneous singing of distinct groups, group composition (number of singers), or individual singing characteristics. When in doubt about whether the same group or 2 distinct groups produced 2 tape-recordings, we excluded the recording of inferior sound quality from the analysis. In Table III we list the number of gibbon groups we recorded at each locality and the number of gibbon groups whose recorded songs were suitable for analysis.

Per tape-recorded individual, we analyzed a maximum of 7 complete and fully developed phrases. If more phrases were available, sonogram quality was the selection criterion. We regarded a male phrase as fully developed if the multimodulated phrase consisted of ≥ 2 notes of which the second exhibited ≥ 1 roll. Aborted great calls lack the twitter and usually comprise <5 notes.

Acoustic Analysis

We measured 22 male and 14 female structural parameters (of the frequency and/or time dimension) from the sonogram of each phrase selected for analysis (Fig. 4). To quantify acoustic characteristics of the male and the female phrase, we defined 84 variables, which are in the Appendix. The reason for calculating that many variables was to adequately describe the complex gibbon song structure without making any assumptions *a priori* on the importance any of the song characteristics may have for discriminating between gibbon populations.

Table III. Localities where tape-recordings were carried out, with names of pooled samples, supposed gibbon taxa occurring at each locality, number, and type of analyzed song bouts

Locality	Pooled samples[a]	Assumed taxon (provisional)[b]	Number of groups		Type of analyzed song bouts	
			Recorded	Analyzed	Duet	Male solo
Bach Ma NP	Bach Ma	*Nomascus leucogenys siki*	8	5	4	1
Taveng District	Virachey	*N. gabriellae*	14	11	10	1
Veunsai District	Virachey	*N. gabriellae*	19	13	9	4
Mas Village	Poey	*N. gabriellae*	3	3	3	0
Khamaeng Village	Poey	*N. gabriellae*	2	1	1	0
Lomphat District	Lomphat	*N. gabriellae*	0	0	0	0
Samling LC Coupe 2A	Samling	*N. gabriellae*	2	2	2	0
Samling LC Coupe 3	Samling	*N. gabriellae*	12	4	4	0
Samling LC Coupe 5	Samling	*N. gabriellae*	1	1	1	0
Total			66	43	37	6

[a]For further analysis, we pooled data from Mas and Khamaeng to 1 sample referred to as Poey.
[b]We assumed gibbons from Bach Ma to be *Nomascus leucogenys siki* because of the close proximity to the type locality of that taxon. All gibbons south of Bach Ma are provisionally identified as *N. gabriellae* because their phenotype resembles this taxon, as far as known.

We based the variables on the measurements taken on the sonograms. All variables of the male song refer to the multimodulated phrases, i.e., the dominant male phrase. We excluded other note types such as booms and staccato notes from the analysis because they are very soft or absent in southern populations of *Nomascus* and thus were often inaudible in our field recordings.

Comparing the Song Structure of *Nomascus leucogenys* and *N. gabriellae*

Geissmann *et al.* (2000) reported differences between the song phrases of *Nomascus leucogenys leucogenys*, *N. l. siki*, and *N. gabriellae,* which we summarize in Table IV. We examined the distinguishing song characteristics in our populations and tested whether the results are consistent with the patterns previously described for *Nomascus leucogenys siki* and *N. gabriellae*.

Statistical Analysis

We performed statistical analyses on a Macintosh G3 via the SPSS software (version 11.0 for Mac OS X). Data for 12 gibbon groups contained

Table IV. Suggested differences in song features among 3 *Nomascus* taxa (after Geissmann *et al.*, 2000, p. 45ff), and results of the qualitative examination of songs of 5 study populations with *N. leucogenys siki* and *N. gabriellae*

				Qualitative assignment of study populations[a]				
Song characteristics	*N. l. leucogenys*	*N. l. siki*	*N. gabriellae*	Bach Ma	Taveng	Veunsai	Poey	Samling
Male song (multimodulated phrase):								
Begin of first note	Long section of rel. stable frequency	Long section of rel. stable frequency	Long section of descending frequency	*g*	*g*	*g*	*g*	*g*
Duration of rolls	Not very fast	Not very fast	Extremely fast, resembling a trill	*s*	*s*	*s*	*s*	*g*
Occurrence of rolls on third note	Common	Rare	Absent or very rare	*g*	*g*	*g*	*g*	*g*
Female song (great call phrase):								
Number of barks	15–30 notes (up to 39)	8–18 notes	5–13 notes	*s*	*s*	*s*	*s*	*g*
Start frequency of great call notes	Low	Low	High	*g*	*g*	*g*	*g*	*g*
Start frequency across all great call notes	Constant	Constant	Ascending	*g*	*g*	*g*	*g*	*g*

g = Nomascus gabriellae; *s* = Nomascus leucogenys siki.

missing values if vocal data for only 1 sex were available as a result of solo singing or poor sonogram quality of 1 duet partner's contributions. Some males never uttered >1 roll in their second note, and therefore variables describing multiple rolls are not applicable to the individuals. Most multivariate analyses reject all data sets with a missing value. To be able to use the sample of all 40 recorded gibbon groups, we replaced the missing values in the data matrix by the overall mean for that particular song variable.

Discriminant Function Analysis

We used stepwise discriminant function analysis (DFA) to identify differences in vocalizations among the 5 gibbon populations (Samling Logging Concession, Poey, Veunsai, Taveng, and Bach Ma), which permits study of group differences with respect to several variables simultaneously. Redundancy among the independent variables is avoided via a tolerance test, which measures the degree of linear association between variables. A variable that is almost a linear combination of a variable already in the model is excluded from the analysis. For the stepwise procedure, we determined Wilks' lambda as the criterion for variable selection. To test the significance of the change in the selection criterion when we entered or removed a variable from the model we used the probability of F and applied $p\text{-}to\text{-}enter = 0.05$ and $p\text{-}to\text{-}remove = 0.1$ as significance levels. This allowed us to screen out variables that were less efficient discriminators and to identify the combination of song features that best discriminated among the study populations. Based on the selected variables, several linear functions (discriminant functions) were formed that we in turn used for the classification procedure that assigned each gibbon group to its appropriate population (correct assignment) or to another population (incorrect assignment). We used the percentage of correct assignments as an indicator of the discriminability of populations and calculated Cohen's κ to test whether the resulting classification significantly differed from chance (Siegel and Castellan, 1988). The model derived from the analysis was cross-validated by the leaving-one-out method (Norusis, 1994), which involves leaving out each of the cases in turn, calculating the functions based on the remaining $n - 1$ cases, and then classifying the left-out case.

Multidimensional Scaling

We used multidimensional scaling (MDS) to visualize (and to further analyze) the existing vocal similarities or dissimilarities (distances)

between the recorded gibbon groups. We used Kruskal's Stress measure as goodness-of-fit index to estimate the quality of the MDS configuration compared to a perfect representation of the actual vocal distances between gibbon groups. The Stress measure ranges from 1 (worst possible fit) to 0 (perfect fit). MDS plots are better suited to visualize multivariate relationships in 2-dimensional plots than discriminant functions are because the resulting plots exhibit a much lower degree of distortion (Manly, 1994; Sneath and Sokal, 1973). Therefore we used MDS plots to estimate vocal distances and vocal variability within gibbon populations.

RESULTS

Vocal Differences Between *Nomascus leucogenys siki* and *N. gabriellae*

The sonograms in Fig. 5 are excerpts of duet song bouts from each focal gibbon population. Based on the vocal differences between crested gibbon taxa that Geissmann *et al.* (2000) described, we qualitatively assigned songs of the 5 populations to either *Nomascus leucogenys siki* or *N. gabriellae* (Table IV). Whereas we consistently identified the Samling population from southeastern Cambodia as *Nomascus gabriellae* in all 6 criteria, we identified the Bach Ma population from central Vietnam and the 3 northeast Cambodian populations (Taveng, Veunsai, and Poey) as *N. gabriellae* by 4 criteria and as *N. leucogenys siki* by the other 2.

Discriminant Analysis

Of the 84 song variables analyzed, we included 9 in the discriminant model by the stepwise procedure (variables 30, 34, 38, 43, 47, 49, 59, 72, and 83; Table V); the subset is most efficient in distinguishing among the songs of the 5 gibbon populations. The standardized canonical discriminant function coefficients of the key variables (Table VI) estimate the relative contribution of a given song variable to the 4 discriminant functions, i.e., the reclassification of gibbon groups into populations. High absolute values represent a large relative contribution.

Discriminant analysis created 4 functions (1 fewer than the number of groups). The functions differ in their merits for group separation. The first function normally contains the highest discriminatory power and the last function the lowest. The discriminatory strength can be expressed by the percentage of between-groups variability attributable to a specific function. The first discriminant function made the highest contribution by far to

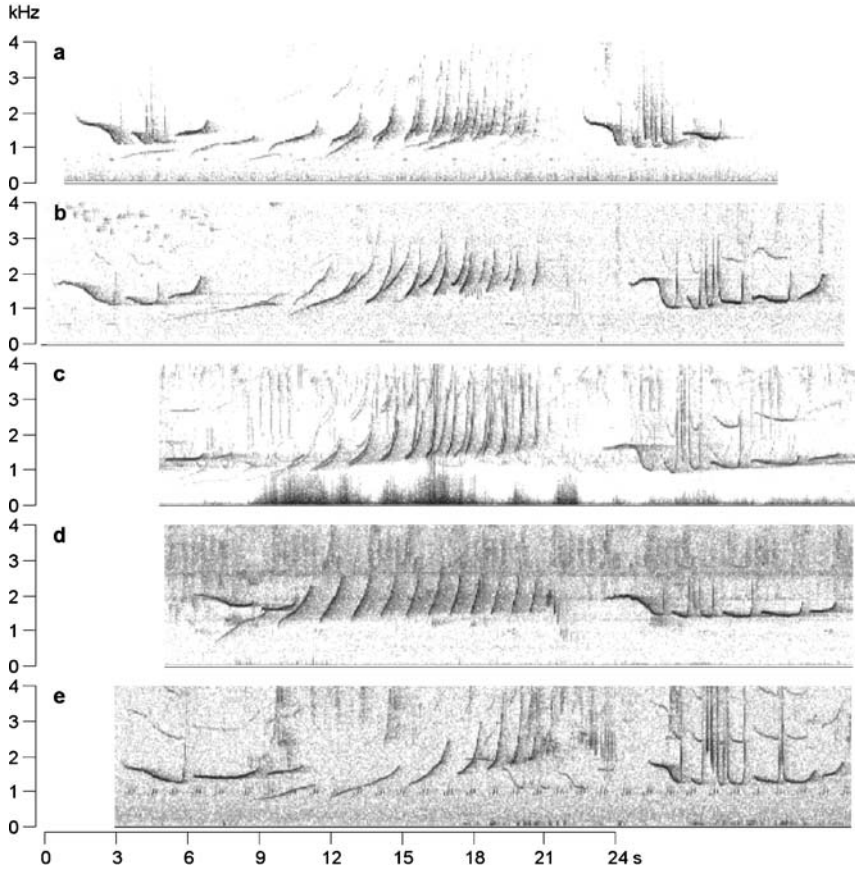

Fig. 5. Sonograms of excerpts of song bouts from different gibbon groups and different populations. All sonograms shown originate from duet songs and exhibit 1 complete great call sequence consisting of 1 fully developed female phrase followed by a male phrase. Recording localities are ordered from north to south: **(a)** Group 74 from the Bach Ma National Park in Thua Thien Hue Province, central Vietnam; **(b)** group 25 from the eastern part of Virachey National Park (Taveng District) in northern Rattanakiri Province, Cambodia; **(c)** group 12 from the central part of Virachey National Park (Veunsai District) in northern Rattanakiri Province, Cambodia; **(d)** group 35 from Poey Commune in central Rattanakiri Province, Cambodia; **(e)** group 48 from the Samling Logging Concession in southern Mondulkiri Province, Cambodia.

separate the 5 gibbon populations by explaining 74.5% of the total variability, whereas functions 2, 3, and 4 contributed progressively less (13.5%, 8.8%, and 3.2%, respectively).

Figure 6 is a 2-dimensional plot of all gibbon groups according to their discriminant score for the first and the second discriminant function and

Table V. Definitions of variables selected for discriminant analysis by the stepwise procedure

No	Variable (unit)	Description of variable
Multimodulated phrase of the male		
Note 2		
30	Relative duration of roll part (%)	Duration of roll part in% of duration of second note
34	Duration of terminal part (s)	Duration of the post-roll part of second note (see terminal part in Fig. 4)
38	Minimum frequency (Hz)	Minimum frequency anywhere in second note
43	Frequency range to first trough in roll part (Hz)	Frequency range from minimum frequency in pre-roll part of second note to the local frequency minimum between the first and the second up-down sweep (roll) of the roll part (measurement *h* in Fig. 4)
47	Minimum frequency of terminal part (Hz)	Minimum frequency of post-roll part of second note (at measurement point *K* in Fig. 4)
Note 3		
49	Number of rolls	Number of up-down sweeps in roll part of third note
Note 4		
59	Frequency range (Hz)	Frequency range from minimum frequency anywhere in the fourth note (if present) to maximum frequency reached in any part of the note except in rolls or the terminal up-sweep of the note
Great call phrase of the female		
72	Duration of first *oo* note (s)	Duration of the first note of the female phrase (measurement *s1* in Fig. 4)
83	Second start frequency range (Hz)	Frequency range from start frequency of second note of the female phrase to start frequency of third note (frequency range between measurement points *T* and *R* in Fig. 4)

illustrates the degree of separation among the overall mean scores of each gibbon population. Discriminant function 1 mainly separates the Samling population from the rest of the samples, whereas discriminant function 2 elucidates differences among the populations from Poey, Veunsai, Taveng, and Bach Ma. Samling is the most distinct of our study populations.

The results of the reclassification procedure are in Table VII. The overall percentage of gibbon groups correctly assigned to their population is 92.4%. The accuracy of reclassification of gibbon groups to populations ranged from 80% for the Bach Ma population to 100% for the Samling, Poey, and Veunsai populations. The obtained assignment differed significantly from chance (Cohen's $\kappa = 0.90$; $p < 0.000$). The results of our multivariate analysis of vocal characteristics show that local gibbon populations have their own vocal identity and can clearly be distinguished from each other. All 3 cases of wrong assignment occurred among the 3 northernmost

Table VI. Standardized canonical discriminant function coefficients for all 4 discriminant functions[a]

Discriminant function	Variable Nr								
	30	34	38	43	47	49	59	72	83
1	0.47	0.85	0.53	0.59	−0.69	0.61	0.91	−0.57	0.91
2	0.91	−0.02	−1.76	0.34	1.98	0.64	0.45	0.31	−0.24
3	0.03	−0.61	0.74	0.51	0.23	−0.29	−0.16	0.61	−0.06
4	0.92	0.55	0.64	−0.004	−1.00	−0.69	0.51	−0.28	−0.38

[a]Variables are identified by their variable numbers and are listed in the same order as included in the analysis.

samples: The classification procedure incorrectly assigned 2 groups from Taveng to the Veunsai population and 1 group from Bach Ma to the Taveng sample, indicating (Table VII and Fig. 6) that vocal differences among them are less pronounced than those between Samling and the other samples.

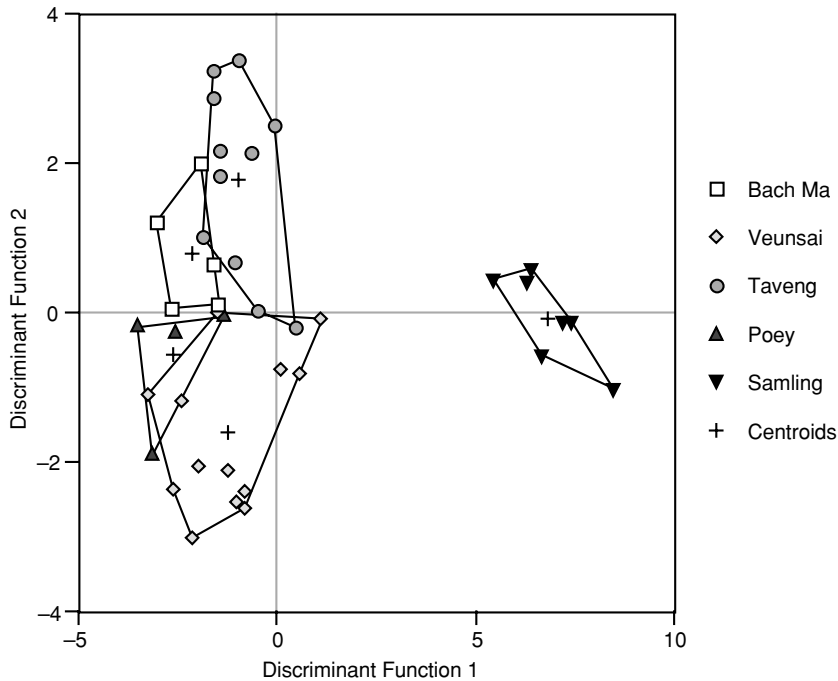

Fig. 6. Discriminant scores of all gibbon groups. Different populations are identified with different symbol shapes. Crosses indicate population centroids.

Table VII. Classification results of discriminant analysis

Population Nr		Groups assigned to population 1	2	3	4	5	% of groups correctly classified	Total number of groups
Original classification								
1	Samling	7	0	0	0	0	100	7
2	Poey	0	4	0	0	0	100	4
3	Veunsai	0	0	13	0	0	100	13
4	Taveng	0	0	2	9	0	81.8	11
5	Bach Ma	0	0	0	1	4	80	5
	Total	7	4	15	10	4	92.4	40
Cross-validated classification								
1	Samling	7	0	0	0	0	100	7
2	Poey	0	3	0	1	0	75	4
3	Veunsai	0	1	7	3	2	53.8	13
4	Taveng	0	0	3	7	1	63.6	11
5	Bach Ma	0	0	1	1	3	60	5
	Total	7	4	11	12	6	70.5	40

We used all song material (duet and solo phrases). We obtained the original classification when we classified groups by the functions derived from all groups (n). In the cross-validation, we classified each group by the functions derived from all groups other than that group ($n-1$).

The cross-validation produced an overall classification accuracy of 70.5%, which is 22% lower than for the original classification. Despite the lower classification accuracy in the cross-validation, the classification results still differ significantly from chance (Cohen's $\kappa = 0.58, p < 0.0001$). Whereas the proportion of correctly identified gibbon groups in the Samling population remained at 100% in the cross-validated classification, the values declined in all other populations, suggesting that the latter are less distinct populations than Samling.

Multidimensional Scaling and Intrapopulation Variability

Figure 7 is a 2-dimensional representation of the vocal similarities among the recorded gibbon groups resulting from the MDS procedure (Stress = 0.29). Points that are close together stand for gibbon groups that are vocally very similar to each other, and large distances on the map indicate great dissimilarity among the respective gibbon groups. The position of the population centroids and the amount of overlap among the population polygons represent the degree of similarity among the 5 populations. Similar to the plot of the discriminant functions (Fig. 6), the values for the gibbon groups from Samling lie apart from those of all other populations. The

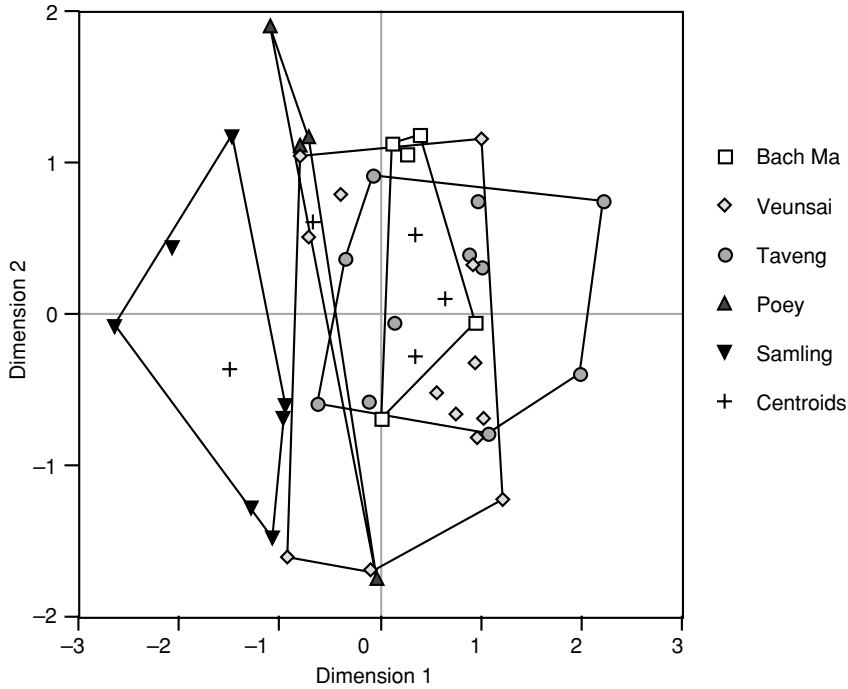

Fig. 7. Two-dimensional display representing similarity, as determined by multidimensional scaling (MDS). Symbols represent individual gibbon groups. Different populations are identified with different symbol shapes. Crosses indicate population centroids.

clusters and centroids for the populations from Poey, Veunsai, and Taveng are closer to each other than any of them is to Samling. To evaluate intrapopulation variability of our samples, we determined the Euclidean distance of each gibbon group to the MDS centroid of its respective population (Table VIII) and compared the values via ANOVA. The differences are not statistically significant ($df = 4$, $p = 0.657$), indicating that song variability is similar in each of our populations.

Vocal *vs* Geographic Distance

We measured geographic distance as the minimum distance between the recording sites and represented the position of each population (Table I) with the coordinates of 1 particular recording position. We

Table VIII Vocal variability in every study population, measured as the variability of Euclidean distances of all gibbon groups from their respective population centroid in the MDS plot

Population	Number of gibbon groups	Mean distance from centroid	Standard deviation	Coefficient of variation
Bach Ma	5	0.790	0.284	0.359
Veunsai	13	1.116	0.488	0.437
Taveng	11	0.975	0.434	0.445
Poey	4	1.224	0.898	0.734
Samling	7	1.011	0.330	0.326

neglected the small distances between the various recording positions when recording gibbon groups of the same population. We averaged the recording positions in Khamaeng village and Mas village (Poey Commune) owing to the relative proximity of the 2 places and the low number of gibbon groups tape-recorded in either of them. We measured the vocal distance between 2 gibbon populations as the distance between their respective centroids on the plot of the MDS analysis (Fig. 7). There is no significant correlation between geographic and vocal distances (Pearson correlation, $r = 0.388$, $p = 0.268$). Yet, a nonsignificant correlation does not exclude that geographic distance has an influence on vocal distances. To exclude any influence of geographic distance, we determined the vocal residuals in a least squares regression between vocal distances (dependent variable) and geographic distances (independent variable). Large positive residuals indicate vocal distances that are larger than expected for their geographic distance, whereas large negative residuals indicate populations that are vocally more similar than expected based on their geographic distance. Relatively large positive residuals occur in dyads including the Samling population, whereas relatively large negative values tend to occur in dyads including the Bach Ma population (Fig. 8).

DISCUSSION

Taxon-Specific Vocal Characteristics

According to the commonly assumed distribution ranges of the taxa, *Nomascus leucogenys siki* and *N. gabriellae* should each be represented in our study with ≥ 1 population (Bach Ma and Samling, respectively). In a qualitative analysis, we examined whether the calls of our study populations consistently matched the previously described vocal characteristics of 1 of the 2 taxa (Geissmann *et al.*, 2000). We then tested whether the

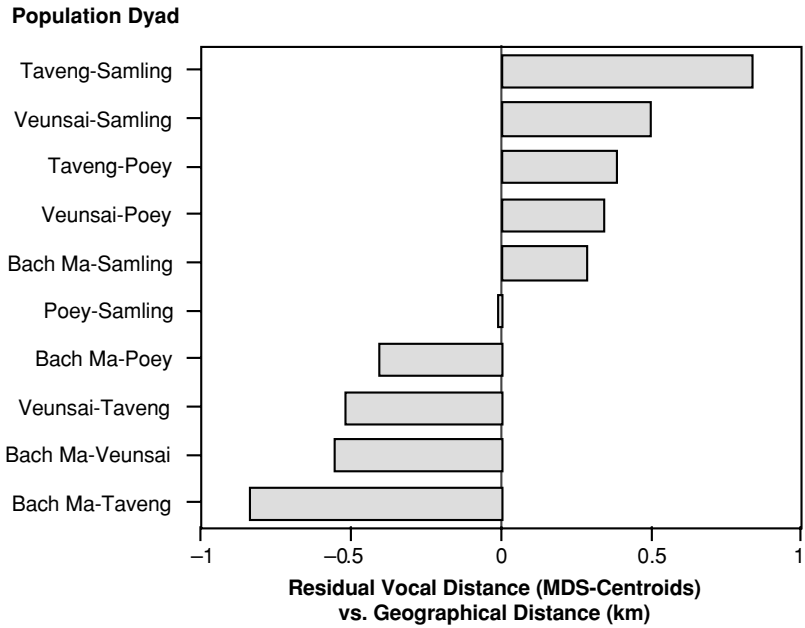

Fig. 8. Residuals of the regression of vocal distance (MDS-centroids) *vs* geographic distance (km).

assignment of populations to taxa based on vocal characteristics corresponded with their assumed distribution ranges of the taxa.

We confirmed a classification of the population from Samling as *Nomascus gabriellae*. The Bach Ma population (central Vietnam) and the populations from Poey, Veunsai, and Taveng (northeast Cambodia) corresponded to the *Nomascus leucogenys siki* in 2 of the criteria and to *N. gabriellae* in the other 4. Additional character states for booms and staccato notes also differ among taxa of *Nomascus* (Geissmann *et al.*, 2000), but they were extremely difficult to confirm in field recordings so we ignored them.

It is clear that 1) the songs from northeastern Cambodia and from Bach Ma qualitatively sound very similar to each other, 2) neither of them completely matches the previously reported taxon-specific song characteristics for *Nomascus leucogenys siki* or *N. gabriellae* (Geissmann *et al.*, 2000), and 3) a convincing identification using the criteria was possible only for the Samling sample (identified thus as *N. gabriellae*).

The description of Geissmann *et al.* (2000) of song differences between *Nomascus leucogenys leucogenys*, *N. l. siki,* and *N. gabriellae* is based on data that also included zoo recordings carried out under optimal conditions,

unlike many of our field recordings. One should especially take into consideration that the vocal criteria for *Nomascus leucogenys siki* are based almost exclusively on zoo gibbons, for which there is uncertainty about the exact origin of an individual (or its ancestors) and thus the exact taxonomic status is problematic. Though songs of zoo gibbons regarded as *Nomascus gabriellae* correspond with songs of wild gibbons in the proposed distribution range of the taxon, the same does not appear to be the case for *Nomascus leucogenys siki*. Consequently, a study is needed to compare song characteristics of *Nomascus leucogenys siki* in zoos with those of individuals living in their natural habitats.

Because Bach Ma is very close to the type locality of *Nomascus leucogenys siki*, Thua Luu (Delacour, 1951), and because no obvious geographic barrier appears to occur between Bach Ma and the type locality, it should be assumed that the gibbons from Bach Ma are, in fact, *Nomascus leucogenys siki*. Further, Bach Ma (at a latitude of *ca.* 16°12′N) is in the assumed distribution range of *Nomascus leucogenys siki* (i.e., between 15°45′N and *ca.* 20°N, according to Groves, 2001). Apparently, the zoo gibbons identified by their phenotype (fur coloration) as *Nomascus leucogenus siki* produce a different song from that of the Bach Ma gibbons. Future studies should examine several possible explanations for our finding, including: 1) Delacour's (1951) holotype may not originate from the type locality. If the researchers simply bought subjects on the market, then the reported phenotype of *Nomascus leucogenys siki* may differ from the actual phenotype of the type locality. It would explain why zoo gibbons identified as *Nomascus leucogenys siki* based on phenotype produce a song that differs from the song of Bach Ma, which is presumably similar or identical to the song of the type locality. It would also explain why a second museum specimen from the same locality, but from a different collector, does not look like *Nomascus leucogenys siki*, but instead like *N. gabriellae* (Geissmann *et al.*, 2000, p. 49). 2) It is conceivable that 2 distinct gibbon populations exist that both exhibit the *Nomascus leucogenys siki* morphotype but that differ in their calls. One would be represented by the Bach Ma population, and possibly include all our northeast Cambodian study populations; the other may be located further to the north and be represented by the zoo gibbons that were the basis of the vocal criteria of *Nomascus leucogenys siki* that Geissmann *et al.* (2000) reported.

Multivariate Analyses of Vocal Diversity

Discriminant analysis shows that it is possible to distinguish the 5 populations on the basis of vocal data with an overall classification

accuracy (percentage of correctly classified group members) of 92.4%. The results imply that considerable vocal diversity exists among at least some of them.

One should interpret results for the population from Poey with caution because of the small sample size and high proportion of groups with missing values, which may lead to biased results if the few groups in the analysis do not represent the entire population. If the population centroid for the discriminant scores is representative for the population in Poey, then one can easily separate the population from all other populations in the sample.

The extent of vocal differences among the study populations is not the same for all pairs of populations compared, and they appear to differ in the expression of population-specific song characteristics. The Samling population is the most distinct sample, whereas the remaining Cambodian populations and the Vietnamese Bach Ma population form a more heterogeneous cluster.

Vocal Distance *vs* Geographic Distance

So far, most researchers on geographic variation and interpopulation variability in primate vocal behavior compared only 2 samples (Arcady, 1996; Fischer *et al.*, 1998; Hafen, 1998; Maeda and Masataka, 1987; Mitani *et al.*, 1992, 1999), which makes it difficult to draw any conclusion on the actual relevance of the observed vocal differences. Comparison of >2 populations reveals more meaningful results, because the differences can be set into relation to one another.

We compared vocal samples from 5 different localities with various geographic distances among them, which allowed for 10 pairwise comparisons. For each pair, the relative amount of vocal differences can be determined, e.g., via multivariate analysis. The degree of vocal differences can indicate the degree of genetic divergence between the populations and the extent to which vocal differences among local populations correspond to the geographic distances. Further, vocal differences can provide useful evidence for determining the position of possible taxonomic and biogeographic boundaries between populations, as in studies on birds, tree frogs, and primates (Baker, 1974, 1975; Dallmann and Geissmann, 2001, 2006; Ralin, 1977).

We compared vocal and geographic distances among populations to evaluate further the taxonomic status of the gibbon study populations, especially in northeast Cambodia. If vocal differences among local populations correspond to geographic distances, they probably reflect random genetic drift. However, a deviation from such a simple relationship could suggest genetic isolation among them.

Table IX. Distance matrices showing geographic (a) and vocal (b) pairwise distances for all gibbon populations

(a) Geographic distance	Poey	Veunsai	Taveng	Bach Ma
Samling	188 km	215 km	217 km	440 km
Poey		30 km	35 km	254 km
Veunsai			32 km	229 km
Taveng				223 km
(b) Vocal distance				
Samling	1.283	1.837	2.182	2.041
Poey		1.345	1.397	1.007
Veunsai			0.486	0.812
Taveng				0.520

Geographic distances are minimal distances between the coordinates of representative recording positions for each study area. Vocal distances are minimal distances between the population centroids of the MDS scores.

We found no significant correlation between vocal and geographic distances. Whereas the geographic distance between Samling and Bach Ma is approximately twice as large as that between Samling and the other 4 populations, the vocal distance between Samling and Bach Ma is in the same range as the vocal distances between Samling and other study populations. In other words, with northeastern Cambodian populations (Poey, Veunsai, and Taveng) as a starting point, the geographic distances to Samling in the south and Bach Ma in the north are approximately the same (*ca.* 200 km), but the vocal distances to Samling are larger than those to Bach Ma in every population dyad (Table IX).

We obtained the same result when we calculated residuals of vocal distances (dependent variable) *vs* geographic distance (independent variable). The residuals should, per definition, represent the vocal differences among populations after one removes any influence of the geographic distance. The residuals (Fig. 9) suggest high relative vocal differences in dyads that include Samling and low relative vocal differences in dyads that include Bach Ma. The finding suggests that an isolation mechanism is operating between the 3 populations in the northeast of Cambodia on one hand and Samling on the other, whereas no such effect is indicated between northeast Cambodia and Bach Ma.

The vocal distance between Poey (our smallest sample) and Bach Ma is closer than what could be expected from the geographic distance. In this respect, Poey resembles the samples from Virachey. Conversely, the vocal distance between Poey and Samling does not appear to deviate from what would be expected based on geographic distance. It is the only result in

which Poey differs from the other northeast Cambodian samples, and it may be influenced by the small sample size available for them.

Possible Taxon Boundary

From maps and observations in the field, we identified 2 geographic features that may serve as distribution barriers between gibbons in northeast and southeast Cambodia and, therefore, may represent the isolation mechanism.

First, the Srepok River is a large tributary of the Mekong River and runs from east to west about 50 km south of Poey Commune (Fig. 2). It separates the northeastern corner of Cambodia from the rest of east Cambodia. The distribution ranges of different gibbon taxa are often separated by rivers (Marshall and Sugardjito, 1986; Morris, 1943; Parsons, 1940, 1941).

Second, the Central Indochina dry forests (CIDF) are dominated by dry, open woodlands and grasslands with interspersed fragments of wetter grasslands and evergreen forest (Legris and Blasco, 1972). Most of this habitat is not suitable for gibbons. Srikosamatara and Doungkhae (1982) proposed that dry dipterocarp forest acts as a barrier to gibbon dispersal in northeast Thailand. The eastern part of the CIDF reaches into central east Cambodia and is encompassed in the east by the rich tropical evergreen forests of the Greater Annamite mountain chain. In 2 areas, the extended evergreen forests reach westward into Cambodia in a semicircular fashion: 1) The Cambodia/Laos/Vietnam triborder forests in the very northeast of Cambodia (including Virachey National Park and Poey Commune) and 2) the western slopes of the Southern Annamites further to the south (including the Samling Logging Concession). Both rain forest areas are separated from each other by extensive areas of open dry forests and grasslands, which may inhibit genetic exchange between the gibbon populations in northeast and southeast Cambodia.

Because the Srepok is a westward-flowing river originating in western Vietnam, it obviously cannot serve as a genetic barrier in eastern Vietnam. Likewise, the CIDF does not expand eastward far enough to split Vietnamese forest types effectively into northern and southern halves. Therefore, further research is needed to determine what, if anything, acts as a dispersal barrier between *gabriellae*- and *siki*-like gibbons in Vietnam.

The San River is a tributary to the Srepok River and flows north of it, separating our 2 study areas in the Virachey National Park (Veunsai and Taveng) from the Poey Commune. The source of San River is the Annamite Mountains near the Cambodian-Vietnamese border and is

between 60 and 100 m wide on Cambodian territory (personal estimate by R. Konrad). Because of its size, the San River was also one of our initial candidates for a gibbon distribution barrier; however, this appears not to be the case.

There is no evidence for the existence of a geographic barrier such as large mountains, rivers, or habitat unsuitable for gibbons between the gibbon groups from Veunsai and Taveng. We therefore regard them as belonging to the same population.

Likewise, in spite of the large distance, there is no apparent geographic barrier between the national parks of Virachey (Veunsai and Taveng) and Bach Ma.

Implications for Population Identity and Hybridization

Vocal variability appears to be similar in all 5 populations, suggesting that our samples contain no hybrid population. As discussed earlier, the Srepok River, the CIDF, or both may serve as a distribution barrier between the gibbons in northeast Cambodia and those in the southeast, e.g., in Samling. To assess the degree of genetic isolation between the 2 populations, it would be essential to have vocal samples from the large area in between. To collect a sample, we visited an area with evergreen forest in Lomphat Wildlife Sanctuary (Fig. 2), but heard no gibbon there. It is uncertain whether the sanctuary still supports gibbons.

Because it was not possible to collect samples in the large area between Virachey National Park and Samling Logging Concession, we cannot determine how and where the distinctive vocal patterns of the northeastern and southeastern gibbon populations replace one another. Is there a more or less sharp boundary between the southern and the northern song pattern, or do the vocal patterns just represent the end points of a more or less extensive cline? The former situation should occur if the respective populations were separated by an efficient barrier to gibbon dispersal; the latter should occur in the absence or weak expression of such a barrier.

The Larger Picture

Based on a comparison of gibbon songs, Geissmann (1995) and Geissmann *et al.* (2000) reported that gibbons in a large area in southern Laos and central Vietnam are neither typical *Nomascus gabriellae* nor typical *N. leucogenys siki*. Our study provides the first evidence that the large

area with the unidentified gibbons is even larger than assumed and extends well into northeastern Cambodia.

Geissmann (1995) and Geissmann *et al.* (2000) proposed that this large area either 1) is inhabited by a previously undescribed gibbon taxon, or 2) represents a large intergrade area between *Nomascus leucogenys siki* and *N. gabriellae*, or 3) a combination of the 2. Our data support hypothesis 1 but not hypothesis 2. Gibbons in southeast Cambodia can be identified as *Nomascus gabriellae*, whereas gibbons in northeast Cambodia are another taxon. They correspond to the song type of gibbons from Bach Ma, which probably represent *Nomascus leucogenys siki*.

Because the previously published description of the song type of *Nomascus leucogenys siki* (Geissmann, 1995; Geissmann *et al.*, 2000) is based on zoo gibons of unknown provenance, their song is not identical to that of the gibbons in Bach Ma (Table IV), which suggests that there may be >1 taxon currently included within *N. l. siki*.

Mitochondrial DNA sequences in captive crested gibbons showed that 3 of 5 *Nomascus leucogenys siki* clustered with *N. leucogenys* and the other 2 with *N. gabriellae* (Roos, 2004), indicating that *N. l. siki* may be a paraphyletic taxon. As a result, Groves (2004) and Roos (2004) proposed that *siki* may be a hybrid between *N. leucogenys* and *N. gabriellae*. As an alternative interpretation of the same finding, and more consistent with our results, we suggest that the different clusters of *Nomascus leucogenys siki* may be geographically separated taxa, representing speciation in progress.

Our results on the vocal diversity of Cambodian crested gibbons do not reliably resolve the identity of the gibbon populations in northeast Cambodia, but provide a first element to the solution of a puzzle. Also needed is information concerning critical pelage coloration (and, ideally, molecular characters) in Cambodian and Bach Ma samples. Researchers should extend future studies to include neighboring areas of Laos and Vietnam. To further elucidate the taxonomy of the crested gibbons in southern Indochina, it is essential to collect data both from proposed contact zones and areas where taxa are assumed to occur in pure form. The data could be relevant to assess the actual degree of mixture (if any) between *Nomascus gabriellae* and *N. leucogenys siki*, to estimate the geographic extent of such an intergrade area, and to identify possible taxonomic boundaries.

CONCLUSIONS

1. Not all crested gibbons in Cambodia exhibit the same song pattern, and they are not one homogeneous population.

2. Song patterns of the southern population (Samling) correspond to the previously described pattern of *Nomascus gabriellae*.

3. Gibbon songs from northeastern Cambodia differ from the previously described patterns of both *Nomascus gabriellae* and *N. leucogenys siki* but correspond to the pattern of the study population from Bach Ma, which we tentatively identify as true *N. l. siki* (compared to the zoo specimens of unknown provenance in earlier studies).

4. Study populations do not differ in vocal variability, thus failing to provide evidence for hybridization.

5. A comparison between vocal and geographic distances among gibbon populations suggests the occurrence of a distribution barrier between southeast and northeast Cambodia, but not among northeast Cambodian populations or between them and the Bach Ma population.

APPENDIX: LIST OF VOCAL VARIABLES

Multimodulated Phrase of the Male

Overall Variables: 1. Number of notes, 2. Duration of entire male phrase (s).

Note 1: 3. Duration of first note (s), 4. Maximum duration (s), 5. Minimum duration (s), 6. Duration of horizontal part (s), 7. Rel. duration of horizontal part (%), 8. Duration of trough part (s), 9. Rel. duration of trough part (%), 10. Start frequency (Hz), 11. Maximum frequency of horizontal part (Hz), 12. Maximum frequency (Hz), 13. Minimum frequency (Hz), 14. Frequency range (Hz), 15. Frequency halfway (Hz), 16. Frequency range to halfway point (Hz), 17. Rel. frequency range to halfway point (%), 18. Duration to maximum bend (s), 19. Rel. duration to maximum bend (%), 20. Frequency at maximum bend (Hz), 21. Duration to peak intensity (s), 22. Rel. duration to peak intensity (%), 23. Frequency at peak intensity (Hz), 24. Frequency range to peak intensity (Hz), 25. Rel. frequency range to peak intensity (%).

Note 2: 26. Duration of second note (s), 27. Duration of initial part (s), 28. Rel. duration of initial part (%), 29. Duration of roll part (s), 30. Rel. duration of roll part (%), 31. Number of rolls, 32. Number of "long" troughs in roll part, 33. Duration of first roll in roll part (s), 34. Duration of terminal part (s), 35. Rel. duration of terminal part (%), 36. Start frequency (Hz), 37. Maximum frequency (Hz), 38. Minimum frequency (Hz), 39. Frequency range (Hz), 40. Minimum frequency of initial part (Hz), 41. Frequency range of initial part (Hz), 42. Frequency at first trough in roll part (Hz), 43. Frequency range to first trough in roll part (Hz), 44. Frequency at

last trough in roll part (Hz), 45. Frequency range to last trough in roll part (Hz), 46. Frequency range to lowest trough in roll part (Hz), 47. Minimum frequency of terminal part (Hz).

Note 3: 48. Duration of third note (s), 49. Number of rolls, 50. Start frequency (Hz), 51. Maximum frequency (Hz), 52. Minimum frequency (Hz), 53. Frequency range (Hz), 54. Internotes frequency range (Hz).

Note 4: 55. Duration of fourth note (s), 56. Start frequency (Hz), 57. Maximum frequency (Hz), 58. Minimum frequency (Hz), 59. Frequency range (Hz).

Great Call Phrase of the Female

Overall Variables: 60. Duration of entire great call (s), 61. Number of notes, 62. Range of start frequencies (Hz), 63. Maximum start frequency (Hz), 64. Number of *oo* notes, 65. Duration of *oo* phase (s), 66. Rel. duration of *oo* phase (%), 67. Number of bark notes, 68. Duration of bark phase (s), 69. Rel. duration of bark-phase (%), 70. Rel. duration of twitter part (%), 71. Duration of inter-phrase interval (s).

Single-note variables: 72. Duration of first *oo* note (s), 73. Frequency range of first *oo* note (Hz), 74. Duration of second *oo* note (s), 75. Frequency range of second *oo* note (Hz), 76. Duration of first bark note (s), 77. Frequency range of first bark note (Hz), 78. Duration of last bark note (s).

Successive notes variables: 79. First inter-note interval (s), 80. Second inter-note interval (s), 81. Last inter-note interval (s), 82. First start frequency range (Hz), 83. Second start frequency range (Hz), 84. Last start frequency range (Hz).

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